Chapter 13

Role of fungi in nitrogen, phosphorus and sulphur cycling in temperate forest ecosystems

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Introduction

The continuing flow of energy through any ecosystem depends upon maintenance of nutrient supplies to the primary producers and since there is only a limited input of nutrients from outside, a balanced cycle within the ecosystem is essential. Three main types of cycle (Fig. 13.1) provide nutrients to the primary producer. The *external geological cycle* involves inputs to the ecosystem from the atmosphere (from natural sources and from pollutants), by weathering of soil parent material and from the addition of fertilizers, whereas losses result from leaching, burning and harvesting. The ***biological cycle*** involves exchange between soil, plants, herbivores and carnivores and the decomposer subsystem. ***Internal cycling*** occurs within these subsystems and within individual organisms, particularly trees. Nutrient cycling within forests has received detailed treatment by a number of authors, including Ovington (1962), Duvigneaud & Denaeyar de-Smet (1970), Borman & Likens (1979), Heal (1979), Miller (1979), Whittaker *et al.* (1979), Swank & Waid (1980), Clark & Rosswall (1981), Cole & Rapp (1981), Heal, Swift & Anderson (1981), yet the specific role of fungi has received much less attention (but see Lindberg, 1981).

The crucial role of fungi in the cycling of nutrients lies in the fact that fluxes of nitrogen, phosphorus and sulphur within the decomposer subsystem and other subsystems are mediated largely by

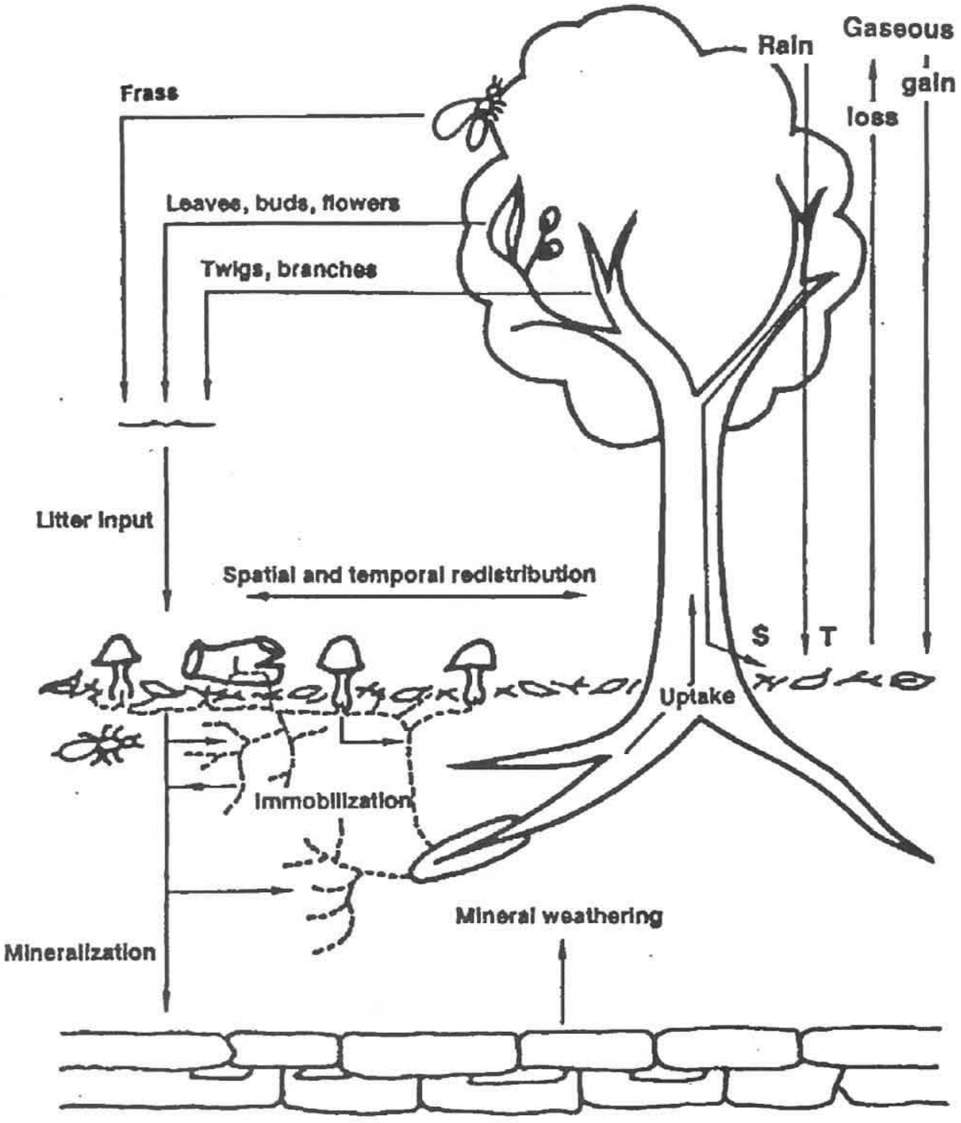

Fig. 13.1. Diagrammatic representation of nutrient inputs, immobilization and mineralization in a forest ecosystem. (S = stem flow; T = throughfall).

them. Fungi, as a result of saprotrophic nutrition, are the major decomposers of organic substrata in terrestrial ecosystems and consequently are responsible for the return of nutrients immobilized in dead plant, animal and microbial tissues to the soil pool. Fungi may also sequester nutrients which have 'leaked' from plants in, for example, the phylloplane and the rhizosphere, and obtain them directly by parasitic interactions. They also directly influence the nutrient relations of autotrophs by the mutualistic association of mycorrhizal fungi and plant roots, and of certain fungi and algae which form lichens. Nutrient fluxes between parasitic fungi and plants are explored by Walters (Chapter 7) and Paul (Chapter 8) and of lichens by Crittenden (Chapter 12), and will not be considered here. The role of mycorrhizas in nitrogen and phosphorous nutrition of plants is treated by Read, Leake & Langdale (Chapter 9), Hetrick (Chapter 10) and Gianinazzi-Pearson & Gianinazzi (Chapter 11), and will only be considered here in terms of their role in saprotrophic decomposition and overall ecosystem nutrient cycling. Emphasis in this chapter will be placed on the role of saprotrophic fungi in nitrogen and phosphorus cycling within temperate forests. Relatively little is known of the involvement of fungi in the sulphur cycle of forest ecosystems but some consideration is given to the possible impact of sulphur depositions arising from atmospheric pollution (see also Wainwright, Chapter 4).

Forest ecosystem development: changes associated with succession

Forests are static neither in space nor time; under suitable climatic conditions, bare ground will be successively covered by herbaceous vegetation and then by woody forms, ultimately forming climax forest communities. The latter are often of uneven age and may be patchy because of localized loss and re-establishment of the canopy. Thus, when considering the role of organisms in nitrogen and phosphorus cycling, it is essential to be aware of the discontinuous and dynamic nature of the ecosystem.

As the seral succession of plant species proceeds, important changes in many aspects of the structure and functioning of the ecosystem occur. Net primary production (NPP) progressively increases and then declines as the climax community becomes established. Associated with the initial increase in NPP is an increase in the total biomass of the system, with an increasing proportion of NPP going into the production of perennial above- and below-ground woody tissues. Associated with the shifts in plant species composition and production of perennial tissues are changes in the quality and quantity of nutrient resources. Thus the standing crop and litter input of herbaceous ground flora decreases, whilst the relative contribution of perennial components increases (Fig. 13.2). This provides increasing and often diversifying opportunities for the decomposer community resulting in a seral succession of the fungal community which will accompany that of the plant community.

Clearly then, dynamics of nitrogen, phosphorus and sulphur cycling processes in an ecosystem will differ according to the successional stage of the system, and changes in the supply of and demand for these elements by the forest (Miller *et al.*, 1979; Miller, 1981; Dighton, 1987; J. Dighton & A. F. Harrison, unpublished) may have significant effects on the physiology of the fungal components of the decomposer community.

Role of saprotrophic fungi in forest nutrient cycling

Input, standing crop and turnover of plant litter and hence nitrogen, phosphorus and sulphur: general considerations

Input and standing crop in temperate forests range, respectively, between 3,700-5,500 kg ha^{-1} yr^{-1} and 11,500-44,500 kg ha^{-1} which represents a large investment of nutrient capital (Table 13.1; Vogt, Grier & Vogt, 1986). Whilst input is largely determined by productivity of green plants, standing crop represents the ratio between input and turnover time, the latter depending on the decomposer organisms, resource quality and microclimate. Above-ground litter comprises various fractions which, in temperate woodlands, are approximately 55% leaves, 10% fruits, buds, flowers, etc., 20% twigs, 10% branches, 5% insect frass and miscellaneous (e.g. Bray & Gorham, 1964; Brown, 1974; Boddy & Swift, 1983). The amount of wood entering the decomposer system has, however, usually been underestimated and a more realistic figure is 40% (Swift, 1977). The input of below-ground

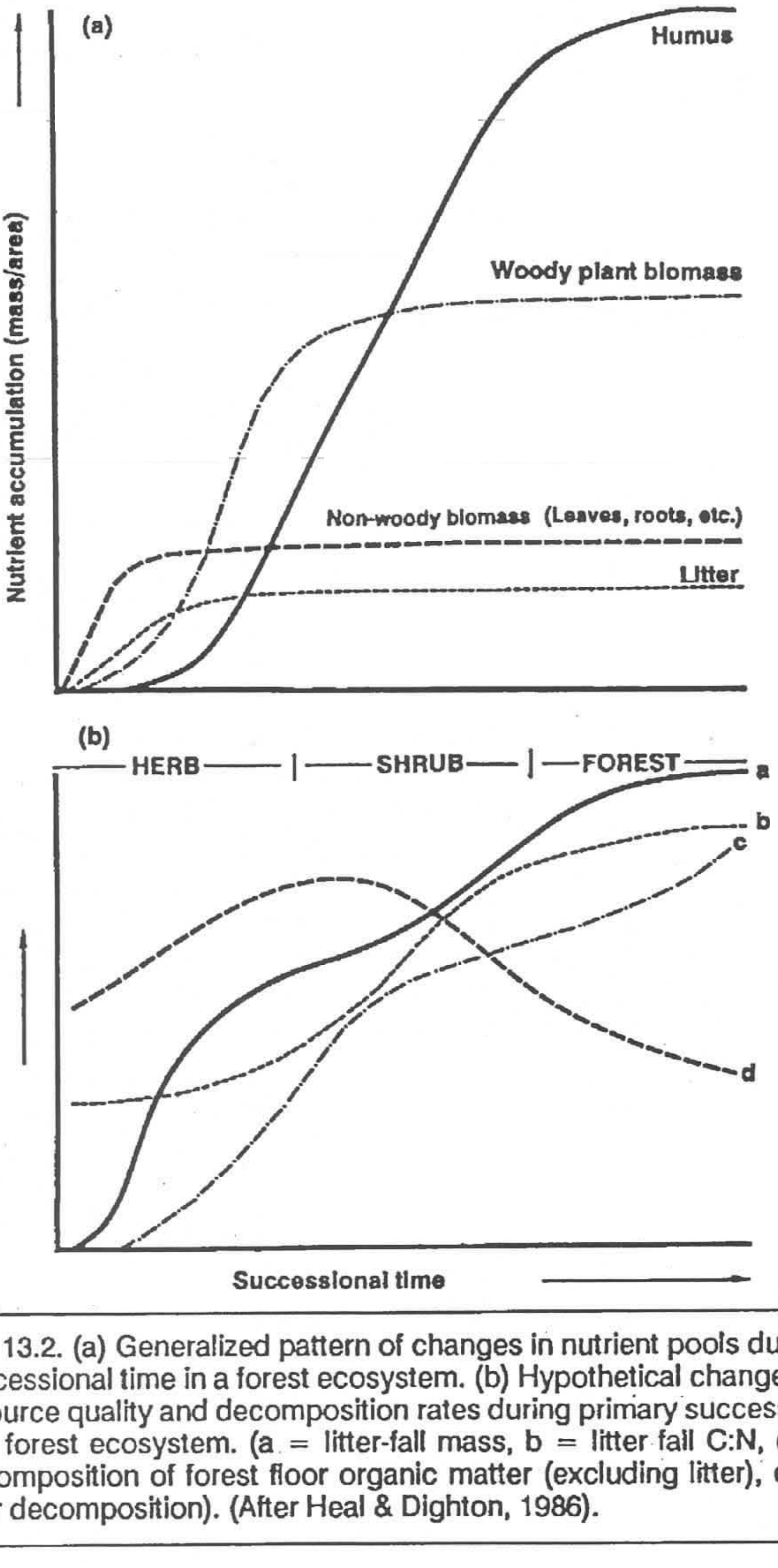

Fig. 13.2. (a) Generalized pattern of changes in nutrient pools during successional time in a forest ecosystem. (b) Hypothetical changes in resource quality and decomposition rates during primary succession in a forest ecosystem. (a = litter-fall mass, b = litter fall C:N, c = decomposition of forest floor organic matter (excluding litter), d = litter decomposition). (After Heal & Dighton, 1986).

Table 13.1. Above ground standing crop and input of nutrients and biomass in woody and non-woody litter in temperate woodlands.

	Forest floor (kg ha^{-1})			Mean residence time on forest floor (yr)			Non-woody litter-fall (kg ha^{-1} yr^{-1})			Woody litter-fall (kg ha^{-1} yr^{-1})		
	biomass	N	P	biomass	N	P	biomass	N	P	biomass	N	P
Warm temperate												
broadleaf deciduous	11,480	163	11·9	2·7	4·8	4·3	4,236	36	3·8	891	2·6	0·8
broadleaf evergreen	19,148	60	3·8	3·1	1·0	2·2	6,484	55	3·7	-	-	-
needleleaf evergreen	20,026	362	25·1	4·6	13·8	11·0	4,432	28	2·7	1,107	2·5	0·2
Cold temperate												
broadleaf deciduous	32,207	624	50·2	10·2	19·1	11·1	3,854	43	4·6	1,046	3·7	0·2
broadleaf evergreen	13,900	200	10·5	3·9	-	-	3,590	-	-	-	-	-
needleleaf evergreen	44,574	504	44·9	17·9	32·8	22·1	3,144	26	3·2	602	1·1	0·1

After Vogt, Grier & Vogt (1986).

biomass is difficult to determine and has frequently been omitted from calculations, but this input can be considerable and must not be ignored (Vogt *et al.*, 1986). Vogt *et al.* (1983), for example, have shown that fine root biomass input to the decomposer community is 200 to 300% greater than leaf litter fall in *Abies amabilis* forests. Similarly, Fogel & Hunt (1983) estimated that for Douglas fir (*Pseudotsuga menziesii*), the return of organic matter to soil by fine roots and mycorrhizas ranged from 78-84% of total tree return, which accounted for over 80% of the total tree return of nitrogen and phosphorus (Table 13.2). Return of nitrogen and phosphorus from mycorrhizas was also estimated to be 4-5 times greater than from other root components (Fogel & Hunt, 1983).

The greatest nitrogen and phosphorus input to the decomposer subsystem is from the non-woody components (Table 13.1) which may sometimes contribute over 35 times that of the woody components. Return of nitrogen and phosphorus immobilized in non-woody litter is also rapid compared to woody components: complete decomposition of most deciduous litter takes between 9

Table 13.2. Standing crops and flux of biomass and nutrients into the decomposer system of a Douglas fir stand.

Component	Standing crop (kg ha^{-1})	Throughput (kg ha^{-1} yr^{-1})	Turnover time (yr)	Release and return of nutrients (kg ha^{-1})[%]	
				N	P
Tree					
foliage	14,732	2,410	6	15·3 [5]	4 [7]
wood	243,396	407	-	3 [1]	2 [3·5]
roots	64,303	$\approx$10,000	1·6	103 [34]	37 [65]
Forest floor	19,034	3,032	6·3	38 [12·5]	2 [3·5]
Fungi					
mycorrhizas	12,794	8,262	1·5	145·5 [47·5]	12 [21]
sporocarps	65	65	1·0		
hyphae	7,035	6,991	1·1		
Stand Total	361,359	31,167		305	57

After Fogel & Hunt (1979, 1983).

months and 3 years, depending on species, with coniferous needle litter taking slightly longer, about 7 years, whereas complete decomposition of twigs, branches and small logs often takes 3 to 20 years and whole trees can take as long as 400 years (Rayner & Boddy, 1988). However, woody material, by virtue of this relatively slow decay rate, forms a large standing crop of biomass. For example, Harmon *et al.* (1986) estimated that the standing crop of large woody components on the floor of deciduous forests was 11 to 38 × 10^3 kg ha^{-1}, and in coniferous forests was 10 to 511 × 10^3 kg ha^{-1} which represents a large reserve of nitrogen and phosphorus. As such, it has been suggested that wood may act as a buffer when systems are perturbed (Ausmus, 1977; Swift, 1977).

Contribution of fungi to decomposition processes and hence to turnover of nitrogen and phosphorus

Decomposition of organic substrata results from a variety of interacting biotic and abiotic factors which can be considered as four distinct processes: non-enzymatic chemical reactions, leaching and/or volatilization, comminution and catabolism (Swift, Heal & Anderson, 1979; Boddy, 1986). Non-enzymatic chemical reactions, such as photosensitized oxidation by sunlight, weakening or direct cleavage of chain bonds by ultraviolet light are probably only significant in exposed situations and may, therefore, be unimportant in woodlands.

Leaching of inorganic ions and, to a lesser extent, soluble organic materials, occurs when water passes through and/or over dead organic substrata and living organisms. Leachates may be captured further down the canopy or soil profile or lost from the ecosystem. Some authors have not found leaching to result in significant weight loss of litter, although others have indicated that losses of 10 to 30% may occur (see Swift *et al.*, 1979; Boddy, 1986). Its significance relative to other components of the decomposition process probably depends on climate (particularly rainfall and temperature), soluble components of different substrata, size and extent of decay, and comminution. With regard to nutrients *per se*, losses can be quite large (Berg & Staaf, 1981). For example, in a mixed deciduous woodland in Belgium, 2 and 20% respectively of the total input of nitrogen and phosphorus at litter fall was attributable to leachate (Duvigneaud & Denaeyer de Smet, 1970). Gosz, Likens & Bormann (1973) found that up to 25% of total nitrogen was leached from *Fagus grandifolia* leaf litter in the field. Volatilization results in loss of oils, waxes, and resins, which will be of significance only in plant litters containing large quantities of these materials, e.g. creosote bush, eucalypts, etc. (Whitford *et al.*, 1981).

Comminution is the reduction in particle size of organic substrata which can be brought about by physical phenomena, such as wetting/drying and freezing/thawing cycles and wind abrasion, but in most ecosystems, including forests and woodlands, invertebrates are the main agents (Swift *et al.*, 1979). Amongst other effects, particle size influences susceptibility to leaching and alters the pattern of microbial colonization with small particles tending to select for unicellular as opposed to mycelial forms (Hanlon & Anderson, 1980; Swift & Boddy, 1984).

Catabolism is the component of decomposition processes which is entirely biologically mediated. Invertebrates catabolize both simple and complex organic molecules, either as a result of their own metabolism or in association with microorganisms, but *quan-*

titatively, their contribution is small, accounting for between about 1 to 15% of total heterotrophic metabolism (Edwards, Reichle & Crossley, 1970), although other invertebrate activities are directly or indirectly much more significant to nutrient cycling. Most of the heterotrophic metabolism in forests, therefore, results from microbial activity. For example, Reichle (1977) estimated that over 85% of the living heterotrophic biomass in a temperate *Liriodendron* forest was microbial. Frankland, (1982) estimated that approximately two-thirds of the total microbial biomass of the litter layer and soil of a temperate deciduous woodland was saprotrophic fungi (i.e. not mycorrhizal nor pathogenic) and amounted to approximately 75 kg ha^{-1}. This figure is, however, not necessarily related to activity, since turnover of bacteria is greater than for fungi. Furthermore, the ability to utilize different components of the litter varies between and within fungal and bacterial groups. With regard to the above- and below-ground woody litter, decomposition is brought about almost entirely by fungi, in particular by basidiomycetes and xylariacious ascomycetes, since they have the capacity to break down the lignocellulose complex, but microfungi are also important at early and late stages of decomposition (Rayner & Boddy, 1988).

Immobilization and mineralization of nitrogen and phosphorus by saprotrophic fungi

It is evident then that the heterotrophic microflora of the forest floor are ultimately responsible for releasing large quantities of nitrogen and phosphorus which would otherwise be retained in plant tissues. 'Ultimately' is, however, the operative word, since before these nutrient elements become mineralized (i.e. made available to the soil pool as soluble inorganic forms) they become immobilized in the fungal tissue of the saprotrophic community. The amounts of nutrients immobilized are dependent upon the group of fungi effecting decomposition of a specific substratum, the resource quality of that substratum and the season. Frankland (1982) estimated that some 30-40% of phosphorus and 18% of nitrogen from *Fraxinus* and *Betula* leaf litter was immobilized by *Mycena galopus* hyphae during incubation for six months. She also demonstrated that immobilization into wood decay fungi can be even greater. Stark (1972) showed that hyphae had 193 to 272%

greater nitrogen content and 104 to 223% greater phosphorus content than needle litter in a temperate *Pinus* forest, which indicated immobilization of these elements. Similarly, Bääth & Söderström (1979) showed that 10%, or 3·8 g m^{-2}, of Norway spruce (*Picea abies*) forest floor nitrogen and 20% of the phosphorus was immobilized into the fungal component.

Nitrogen, phosphorus and sulphur are released from fungal tissues on their death, following lysis or autolysis and during their life by excretion, secretion of extracellular enzymes, leaching and grazing by animals. The lifespan of an organism is, therefore, a major determinant of the duration of the immobilization phase. The lifespan of bacteria and ruderal fungi utilizing ephemeral organic compounds may be only a few days, hence they immobilize nutrients for relatively short periods of time. However, these nutrients may be rapidly sequestered and immobilized by other fungi, particularly if the latter caused the death and lysis of the former. At the other extreme, there are many fungi, almost exclusively basidiomycetes and xylariaceous ascomycetes, which utilize recalcitrant woody substrata and whose individual mycelial systems can persist for several years. Obvious examples include the perennial fruit bodies of certain of the Aphyllophorales, rhizomorphs of certain *Armillaria* spp. and mycelial cords of, for example, *Phanerochaete velutina*, *Phallus impudicus*, and *Tricholomopsis platyphylla* (see Thompson & Rayner, 1982; Dowson, Rayner & Boddy, 1988).

Not only are nitrogen and phosphorus immobilized in fungal structures, but they are also probably relocated within the ecosystem over considerable distances via fungi. Thus, systems of mycelial cords can ramify through leaf litter forming connections between woody and other resources, covering areas of over 2 m^2 (Thompson & Rayner, 1982; Dowson *et al.*, 1988), and individuals of the same genotype of *Armillaria bulbosa* and of *Phanerochaete velutina* have been found decaying dead trees over 50 m apart (Thompson & Boddy, 1983). Large fluxes and rapid rates of translocation (sometimes exceeding 25 cm h^{-1}) of carbon and mineral nutrients have been demonstrated from substrata through cord systems in the laboratory, in the comprehensive studies on the dry rot fungus *Serpula lacrimans* (which is not found in nature)(Watkinson, 1971; Brownlee & Jennings, 1982a & b), and in *Armillaria* sp. (Granlund, Jennings & Thompson, 1985), *Phallus* *impudicus*, *Mutinus caninus* and *Phanerochaete velutina* (Cairney, 1986; J. M. Wells, L. Boddy & J Dighton, unpublished). Rigorous field studies have, however, not been performed.

The implications are that nitrogen and phosphorus are translocated out of organic substrata by cord systems and into substrata which are being colonized. Indeed, such movement of nutrients is likely to occur in all fungi that are capable of mycelial extension out of the substrata in which they are growing. That nitrogen is imported into organic substrata is borne out by the fact that *absolute* concentrations (i.e. amount of nutrient expressed as a percentage of the original quantity or of the volume of the substratum, rather than as a percentage of weight of organic substratum) within leaf and wood litter often increase at early stages of decomposition, particularly in substrata with initially low nitrogen concentrations (Figs. 13.3 & 13.4; e.g. Aber & Melillo, 1980; Berg & Staff, 1981; Melillo, Aber & Muratore, 1982; Swift & Boddy, 1984). However, rigorous field studies are required to determine whether translocation of phosphorus and sulphur to new resources is significant.

Spore dispersal and subsequent colonization is another means of relocating nutrients. For example, spores of *Fomes applanatus* contain 3·05% nitrogen (by dry weight), and it has been estimated by Merrill & Cowling (1966) that all of the nitrogen in 33·7 kg of *Betula alleghaniensis* is required to supply the annual production of the spores of a typical sporophore. The nitrogen in 5·75 kg of wood would be required to produce the sporophore.

The resource as a determinant of rate of mineralization of nitrogen and phosphorus

It was implied above that the lifespan of fungi may be closely related to the degradability of the resource. Hence release of nutrients to the soil pool may largely be governed by the resource itself. The carbon : nitrogen and lignin : nitrogen ratios are known to be determinants of the resistance of substrata to decomposition, and the ultimate release of nutrients has also been explained in terms of these ratios (e.g. Swift *et al.*, 1979; Melillo *et al.*, 1982; Paustian & Schnurer, 1987). At early stages of decomposition the relative concentration (i.e. expressed as % dry weight) of nitrogen and phosphorus tends to increase as the process proceeds, or expressed another way the carbon : nutrient ratio decreases (Figs. 13.3 & 13.4). This occurs irrespective of whether nutrients are imported, because carbon is lost, as CO_2 in respiration, but nitrogen and phosphorus are incorporated into microbial biomass. It has been suggested (e.g. Swift *et al.*, 1979) that net mineralization does

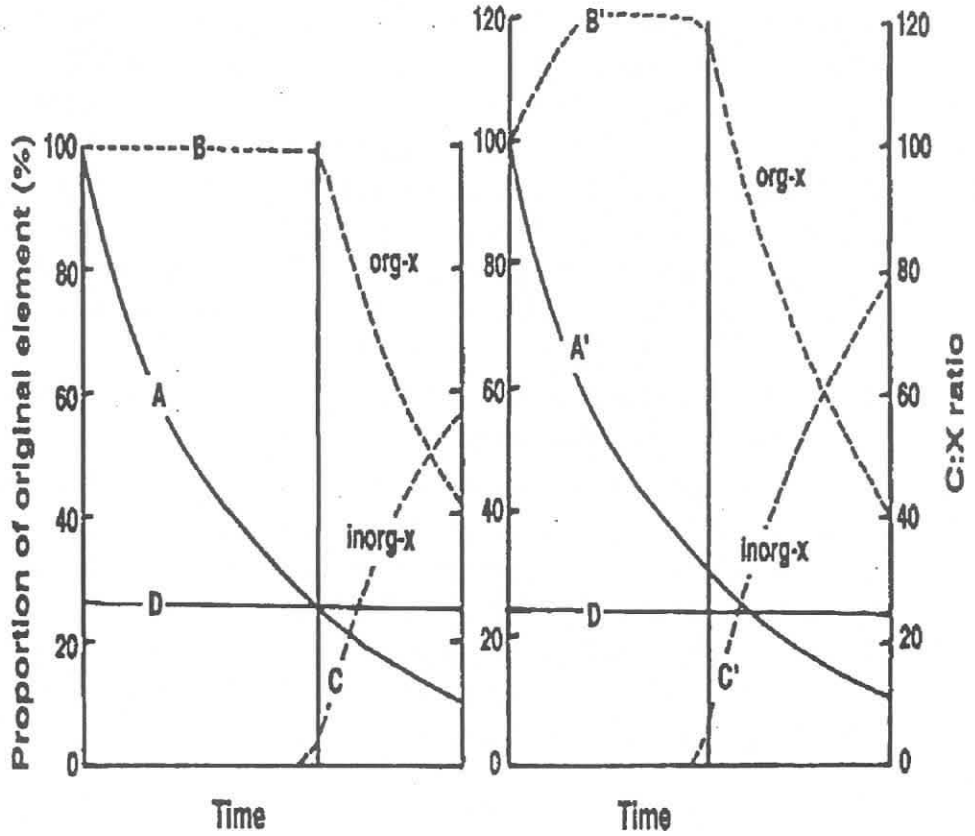

Fig. 13.3. A simple time-course model to illustrate the importance of C:nutrient ratios as indices of the equilibrium between immobilization and mineralization of an element X. Curve A = C:X ratio of an organic resource having an initial ratio of 800:1. Curve B = proportion of X in organic form (immobilised), (Curve B' = case where there is import of X from sources external to the resources being decomposed). Curve C = proportion of X in inorganic form (mineralized), (Curve C' = mineralization in response to alteration of C:X ratio by import of X as in case B'). D = C:X ratio of decomposer organism. After this point net mineralization occurs and curve A flattens off although carbon loss may continue on the same gradient. (From Swift, Heal & Anderson, 1979).

not occur until the carbon : nutrient ratio of the substratum reaches a threshold level which is approximately equivalent to the carbon : nutrient element ratio of the fungus (which is around 15 : 1 for phosphorus and 6 : 1 for nitrogen)(Fig. 13.3; Swift, 1977).

The initial carbon : nitrogen and carbon : phosphorus ratios vary considerably between different litter components. The carbon : nitrogen ratio of undecayed wood typically lies between 350 : 1 and 500 : 1, but can be as high as 1250 : 1, and the carbon : phosphorus ratio is >3500 : 1. In leaf litter these ratios range respec-

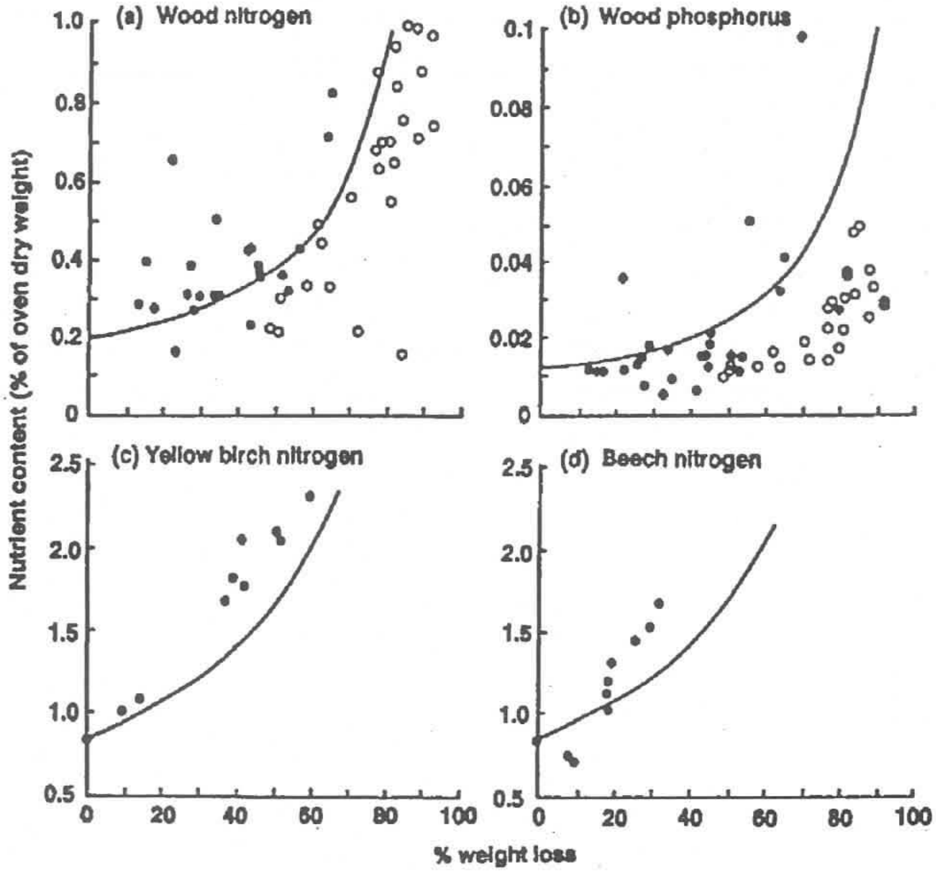

Fig. 13.4. The relationship between mineral nutrient concentration (as % of oven dry weight) and weight loss (% of original dry weight) of wood uninvaded (closed circles) and invaded (open circles) by invertebrates, and of leaf litter (panels c & d). The line on each graph indicates the predicted change in elemental concentration as decomposition proceeds, assuming no net gain or loss. Points above the line therefore represent increase in absolute concentration. [(a) and (b) from Swift & Boddy, 1984; data recalculated from Swift, 1977. Panels (c) and (d) redrawn from Aber & Melillo, 1980; original study by Gosz, Likens & Bormann, 1973].

tively between 25 : 1 to 100 : 1 and 450 : 1 to 1850 : 1 (Cowling, 1970; Swift *et al.*, 1979). Where the ratio is high, as in wood, the decomposer system becomes conservative and with increasing carbon : nutrient ratio there is an increasing trend for the fungi to immobilize nitrogen and phosphorus into their own biomass rather than to effect mineralization. Although the validity of the carbon : nitrogen ratio as a criterion for nitrogen supply is questionable (see Park, 1976; Dowding, 1981; Rayner & Boddy, 1988), it is likely that strong selective pressures act on wood decay fungi for 'economic' use of nitrogen (and phosphorus). As fungi may translocate nutrients it is likely that resources are recycled from 'redundant' hyphae to more active regions. Circumstantial evidence for this possibility is provided by the fact that several wood decay species can utilize their own dead mycelium, and that of other species, as sole source of nitrogen (Levi, Merrill & Cowling, 1968; Jennings, Chapter 1). Cord-forming fungi probably depend largely on 'exploitive' mycelium within the resource to supply the 'exploratory' systems with nitrogen and phosphorus, although it has been suggested that their requirements may be partly met by scavenging nutrients from the soil (Clipson, Cairney & Jennings, 1986). A consequence of efficient internal recycling, at least with cord-forming fungi, is that nitrogen and phosphorus will not necessarily be released to the soil pool when the carbon : nutrient ratio of the wood and the mycelium become similar, but rather will be conserved and translocated elsewhere.

Nitrogen and phosphorus availability may, however, be one factor governing the production of exit structures (i.e. outgrowth of mycelium, cords, rhizomorphs, sporocarps). Although conservation of nutrients is well developed in these fungi this is the part of the system which is 'leaky'. As mentioned earlier, large quantities of nitrogen are removed from wood by production of spores, and since few of these will establish new colonies, much of the nitrogen will be mobilised. Cord systems are also likely to 'leak'. Although no leakage into the soil was detected from major cords of *P. velutina* (L. Boddy & E. M. Owens, unpublished), considerable regression (i.e. dying back) of mycelium has been shown to occur during foraging outgrowth from resources (Dowson, *et al.*, 1986). In particular, mature cords develop following hyphal aggregation within mycelial fronts, with lysis of all hyphae and finely branched cords between the regions of greatest aggregation. Also, when exploratory systems encounter new resources there is often regression of non-connective cords and mycelium which emanate from the 'old' resource. Whilst some of the nutrients may be translocated back into the food base, the remainder will enter the soil pool. Quantitative studies are now necessary before the nutrient dynamics of such systems can be understood.

While carbon : nutrient ratio may partly regulate production of exit structures, at least some species, including cord-forming fungi, produce exit structures from relatively undecayed wood, providing the microclimate is suitable (e.g. Dowson *et al.*, 1986, 1988; Dowson, Boddy & Rayner, 1989). Since some lysis of these reproductive or vegetative structures occurs relatively rapidly, then some mineralization may occur when the carbon : nutrient ratio is still high.

Importance of interactions between soil fauna and fungi in mineralization

The soil fauna is a major determinant of the balance between mineralization and immobilization in organic substrata and microbial biomass, but rather than playing a direct role through catabolism or excretion it influences mineralization by interactions with the microflora (e.g. Anderson & Ineson, 1984). Thus grazing may result directly in release of nutrients as well as altering the relative contribution of different fungal species to the decomposition process (Parkinson, Visser & Whittaker, 1979; Newell, 1984a & b; Swift & Boddy, 1984). At present, however, the functional consequences of alterations in species composition are unclear.

The direct effects of grazing on mineralization and on stimulation/inhibition of fungal respiration and biomass production appear to be variable, probably at least partly because grazing interactions are subject to predator/prey regulation. For example, Visser, Whittaker & Parkinson (1981) found no evidence of enhanced nitrogen mineralization in systems grazed by collembola, and Seastedt & Crossley (1980) suggested that greater immobilization could result from the stimulation of fungal growth by microarthropod grazing. On the other hand there are several examples of increased mobilization of nutrients resulting from animal activity. In a microcosm experiment, Ineson, Leonard & Anderson (1982) found that fungal grazing by the collembolan *Folsomia candida*, on leaf litter, reduced fungal biomass and increased the mineralization of ammonium and nitrate nitrogen (Fig. 13.5). Similarly, consumption of litter (which contains fungi) by larger invertebrates also enhances mineralization. For example, Anderson, Ineson & Huish (1983) investigated the amount of leachable ammonium from microcosms containing oak

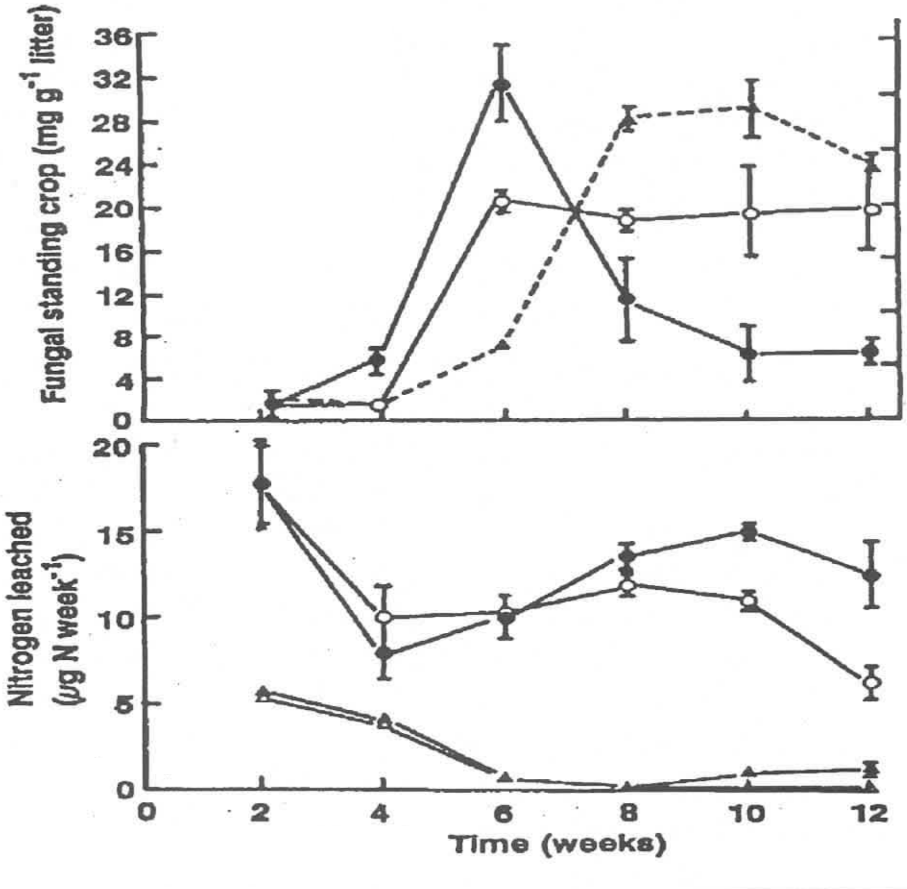

Fig. 13.5. Effect of collembolan feeding activities on fungal standing crop and nitrogen mobilization. (a) fungal standing crop on leaf litter with (closed circles) and without (open circles) collembola, and changes in collembolan populations (triangles); (b) mobilization of nitrogen as ammonium (circles) and nitrate (triangles) in presence (closed symbols) and absence (open symbols) of collembola. Values shown are means ± one SE; n = 4. From Ineson, Leonard & Anderson, 1982.

leaf litter colonised by one of six species of fungi, with and without the millipede *Glomeris marginata*. In all cases mineralization of nitrogen was enhanced in the presence of the millipede, but was strongly correlated with the different abilities of the fungi to effect mineralization. Likewise, enhanced mineralization of sulphur during grazing by the isopod *Oniscus asellus* has been demonstrated by Morgan & Mitchell (1987). Release of nitrogen from wood is strongly correlated with invasion by invertebrates, although appreciable phosphorus appears to occur before animal invasion (Fig. 13.4; Swift, 1977; Swift & Boddy, 1984).

Influence of mycorrhizas on nitrogen and phosphorus dynamics in the soil/plant system

Since much of the assimilable nitrogen and phosphorus in forest ecosystems is immobilized in living and dead plant biomass, the availability of nutrients for further plant growth depends upon recycling within the plant and mineralization by saprotrophic and pathogenic fungi. However, as implied earlier, nitrogen and phosphorus may be immobilized in fungal tissue for considerable periods before becoming available to plants. At early successional stages, nutrients may be relatively more available compared to mature woodlands, especially on poor soils, where the growth of trees is highly dependent on the release of nutrients from organic matter (Miller, 1979; Dighton, 1987; J. Dighton & A. F. Harrison, unpublished). In mature woodland tree roots tend to form associations with ectomycorrhizal fungi (Read, 1986). These not only take up inorganic nitrogen and phosphorus compounds, but can also utilize simple organic molecules (see Read, Leake & Langdale, Chapter 9). More importantly, some mycorrhizal species may be able to act as decomposers and thus short circuit the mineralization/nutrient uptake cycle (Went & Stark, 1968).

There is recent evidence that some ectomycorrhizal fungi have the ability to decompose organic forms of phosphorus and nitrogen by producing extracellular enzymes such as polyphenol oxidases (Giltrap, 1982), phosphatases (Alexander & Hardy, 1981; Ho & Zak, 1979; Dighton, 1983), cellulases (Linkins & Antibus, 1981) and proteinases (Abuzinadah & Read, 1986a & b; Abuzinadah, Finlay & Read, 1986; Dighton, Thomas & Latter, 1987). The ability of ectomycorrhizal fungi to produce degradative enzymes is probably related to the availability of nutrients in the soil. In general, coniferous forests planted on nutrient poor soils increasingly immobilise nutrients as the crop grows. There is a peak of immobilization around canopy closure where nitrogen and phosphorus are not released from organic complexes in the soil at a sufficient rate to supply the tree's demand (Miller, 1979; J. Dighton & A. F. Harrison, unpublished). With an increase in the organic : inorganic ratio of nutrients, the induction of decomposer activity in the mycorrhizal fungal flora would be of importance to the tree crop in the direct procurement of nutrients from organic sources.

It has been suggested by Dighton & Mason (1985) that change in the organic : inorganic ratio of soil nutrients may be one of the forces influencing mycorrhizal fungal succession in that the late stage fungi with '*K*-' strategies have the enzymatic capabilities that the '*r*-' fungi do not. Supporting evidence comes from the data of Abuzinadah & Read (1986a) of growth of eight mycorrhizal fungi on protein, where it was the late stage fungi *Suillus bovinus*, *Rhizopogon roseolus* and *Amanita muscaria* which grew better than the early stage fungi *Laccaria laccata* and *Lactarius rufus*. Similarly, in a gnotobiotic experiment, the decomposition of organic substrates (hide powder and cellulose) was greater in the presence of *Suillus luteus* than *Hebeloma crustuliniforme* (Dighton *et al.*, 1987).

Counter to the opinion that mycorrhizal fungi may be involved in the direct release of nutrients from organic sources, Janos (1983) suggested that it is the juxtaposition of mycorrhizal and saprotrophic hyphae which enables mycorrhizas to remove mineralized nitrogen and phosphorus before they can enter the measurable soil nutrient pool. It is important, therefore, to consider the role of mycorrhizas in the decomposition of organic substrata and acquisition of nutrients from these and recalcitrant inorganic forms in relation to the total soil microbial population. These interactions were explored by Gadgil & Gadgil (1971, 1975) who demonstrated that the presence of mycorrhizal roots suppressed decomposition of needle litter in a *Pinus radiata* forest. However, Berg & Lindberg (1980) repeated these experiments but were unable to detect suppression of litter decomposition in the presence of mycorrhizal roots in a *Pinus sylvestris* forest.

Other interactions between mycorrhizas, saprotrophic organisms and soil fauna are also important. For example, where ectomycorrhizal fungi develop together with bacteria in controlled experiments, they synergistically enhance phosphate uptake by the host pines from recalcitrant inorganic and organic forms (Chakly & Berthelin, 1982; Laheurte & Berthelin, 1986). In an interaction study of the ability of mycorrhizal fungi to decompose organic resources in the presence of a saprotrophic fungus, Dighton *et al.* (1987) showed that the saprotroph inhibited the decomposition potential of the mycorrhizal fungus. Recently, Gransaull & Brown (1987) have shown the synergistic effect of adding both mycorrhizas and *Frankia*: these significantly increased the growth of *Pinus* and *Casuarina* species compared with plants with either mycorrhizas or nitrogen fixing actinomycetes alone. However, much work on such interactions is necessary to evaluate their importance in nutrient mineralization and nutrient sequestering by plants.

Effects of exogenous inputs of pollutants on nutrient cycling

Effects of exogenous nutrient inputs on the forest ecosystem fall into three main types: damage to plants; interactions with fungi; and direct nutrient effects. Pollutant gases may cause physical damage to the canopy foliage and premature leaf fall. This causes a temporal shift in the pulse of nutrient input into the soil system and can also affect the resource quality of the litter. These may in turn influence the rate of decomposition and microbial community structure and consequently nutrient cycling. For example, P. A. Wookey (personal communication) has shown that increasing the atmospheric SO_2 concentration in the range of 10 to 50 ppb significantly reduced microbial respiration in both mixed deciduous and pine leaf litter and altered the rate of mineralization of major nutrients. Sulphur dioxide has also been shown to affect differentially the growth of fungi, e.g. at concentrations of 15 to 50 ppb *Trichoderma* spp. increased, whereas both *Cladosporium cladosporioides* and *Coniothyrium olivaceum* decreased. In addition, atmospheric SO_2 can be used by fungi as a source of sulphur, with different species immobilizing sulphur at different rates (Craker & Manning, 1974; Wainwright, Chapter 4). However, these processes are only just beginning to receive attention. Atmospheric pollutants also affect plants, which act as nutrient sinks, by influencing the species composition and physiology of mycorrhizas (Ulrich, Mayer & Khanna, 1979; Hütterman, 1982; Becker, 1982; Stroo & Alexander, 1985; Reich *et al.*, 1985; Jansen, Dighton & Bresser, 1988). For example, 'acid rain' caused soil chemical changes (Dighton & Skeffington, 1987) and acidified stemflow (Kumpfer & Heyser, 1986), which was correlated with a decreased frequency of corralloid mycorrhizas. Although the nutritional consequences of this imbalance have not been studied in detail, this community shift may represent a movement from '*K*-' to '*r*-' selected fungi and consequently a potential loss in the ability of the mycorrhizal system to sequester nutrients from organic resources in the soil. These effects may be due to mobilization of aluminium and Thompson & Medve (1984) demonstrated that aluminium concentrations of 146 μM could significantly reduce linear growth of agar cultures of the mycorrhizal fungi *Cenococcum*, *Pisolithus*, and *Thelephora*. Also, Oelbe-Farivar (1985) showed that aluminium toxicity reduced protein synthesis in mycorrhizal fungi.

Similarly, there is indirect evidence from the Netherlands that atmospheric nitrogen pollution can significantly affect the succession of mycorrhizal fungi under coniferous trees. By comparing recent fungal fruit body surveys with historical fungal foray records, Arnolds (1985, 1988) has demonstrated a trend of reduction in frequency of occurrence of late stage mycorrhizal fungal fruit bodies, which he attributes to an increase in nitrogen deposition. Also, numbers of *Russula* spp. fruit bodies in beech woods have been found to decline following the application of NPK fertilizer (Hall, 1978). Although care must be taken when interpreting such data (increasing nitrogen content of growth medium *in vitro* typically inhibits fruiting, but not production of mycelial biomass), the effects on plant nitrogen uptake of any such decline in mycorrhizas may be balanced by exogenous inputs of nitrogen which ameliorate conditions on poor soils. If, however, other major nutrients, such as phosphorus, do not increase concomitantly, imbalances could occur, resulting in a reduced yield of the tree crop.

Fungal conversion of inorganic N, P and S compounds

In addition to their saprotrophic abilities, some fungi are able to convert inorganic nitrogen, phosphorus and sulphur compounds from one form to another. Nitrogen exists in a number of interconvertible inorganic forms:

$$N_2 \leftrightarrow N_2O \leftrightarrow (NO) \leftrightarrow NO_2^- \leftrightarrow NO_3^- \leftrightarrow NH_4^+$$

and there is evidence that certain fungi can perform nitrification (i.e. convert NH_4^+ to NO_3^-) e.g. *Penicillium citrinum*, *P. nigricans*, *Cladosporium herbarum*, *Verticillium lecanii* and several members of the genus *Aspergillus*, of which *A. flavus* has received most attention (e.g. Balasubramanya & Patel, 1980; Killham, 1986; Lang & Jagnow, 1986). Several different pathways of heterotrophic nitrification have been postulated and although it is uncertain which operates, it seems unlikely that energy is gained from the process (Killham, 1986). Thus, the benefits of nitrification are unclear. However, it has been suggested that nitrification may provide competitive advantages as certain of the products are known to be toxins, mutagens and microbial growth factors. Whilst it has been shown that the relevant fungi have the ability to nitrify following inoculation into autoclaved soil (Doxtader & Rovira, 1968), there does not appear to be any direct evidence that fungi play a significant role in nitrification in natural soils (Wainwright, 1988). Bacteria are assumed to be the major agents of nitrification (Keunen & Robertson, 1988), however, in acid coniferous forest soils the microbial biomass is often predominately fungal and fungi are believed to play a role in these situations (Killham, 1986).

Some fungi are also capable of nitrate reduction (i.e. convert NO_3^- to NH_4^+) (see also Jennings, Chapter 1; Tomsett, Chapter 2), e.g. *Aspergillus nidulans* and *Neurospora crassa* possess dissimilatory nitrate reduction pathways. Also, a number of species in the genera *Acremonium*, *Aspergillus* and *Fusarium* can perform various steps in the denitrification process (i.e. convert NO_3^- to other nitrogen oxides and dinitrogen) (Bleakley & Tiedje, 1982). These fungi cannot necessarily effect all steps of the process, for example, *Fusarium oxysporum* and *F. solani* can reduce nitrite to nitrous oxide at low oxygen tensions but are unable to reduce nitrate (Bollag & Tung, 1972). As with nitrification, fungi are only likely to make a significant contribution to denitrification in acid forest soils (Bleakley & Tiedje, 1982).

It has in the past been suggested that fungi can fix atmospheric dinitrogen, but Millbank (1969) reappraised the evidence and came to the conclusion that this was not so. More recently, work of Ginterova & Gallon (1979) indicated that the wood-rotting fungus *Pleurotus ostreatus* could reduce dinitrogen to ammonia. However, their results are open to several criticisms and the ability to fix dinitrogen remains unproven (Wainwright, 1988). Even if some species can fix dinitrogen it is likely to be quantitatively insignificant, but they may influence fixation in other ways. For example, Jenson & Holm (1975) have demonstrated that a number of soil fungi stimulate bacterial dinitrogen fixation.

Oxidation of inorganic sulphur compounds is analogous to nitrification of ammonia and nitrate, and a number of fungi are capable of oxidizing elemental sulphur and reduced sulphur compounds. The significance of these transformations to the organisms involved and to nutrient cycling remain unclear, but possibilities are considered by Wainwright (Chapter 4).

With regard to inorganic phosphorus, some fungi are able to release phosphate from insoluble inorganic phosphates, for example, species of *Aspergillus*, *Fusarium*, *Penicillium* and *Sclerotium* produce organic acids and/or chelating components which act as solubilising agents (Beever & Burns, 1980; Wainwright, 1981). Some mycorrhizal fungi are also known to have this ability (Gianinazzi-Pearson & Gianinazzi, Chapter 11). There is some evidence that some fungi, e.g. *Aspergillus niger*, *Alternaria* sp., *Chaetomium* sp. and *Penicillium notatum*, but not others, e.g. *Pythium debaryanum* and *Rhizoctonia solani*, can utilize phosphite as a source of phosphorus. The quantitative significance is again unclear but probably small, particularly as phosphites and hypophosphites are found only in small quantities in soils (Beever & Burns, 1980). Condensed phosphates are widespread in soils arising from physicochemical processes, living organisms and some fertilizers and detergents (Beever & Burns, 1980). Many fungi, e.g. *Aspergillus niger*, *Coprinus lagopus* and *Phytophthora parasitica*, are capable of utilizing pyrophosphate as sole sources of phosphorus.

Whether fungi can utilize condensed phosphates containing three or more phosphorus units is unclear (Beever & Burns, 1980).

Conclusions

Fungi are the major agents of organic matter decomposition in temperate forests and as such play a key role in releasing inorganic nutrients through mineralization. They do, however, immobilize nutrients, often for long periods, in their own biomass and the balance between immobilization and release is often very much dependent on interactions with other organisms, e.g. bacteria, fauna and plant roots. Fungi also participate in inorganic conversions and are affected by exogenous inputs. However, there is little quantitative information on the role of fungi in the dynamics of nutrient cycling. It is essential to the management of forest soil as resource for future crops that this situation is remedied.

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